

NOTES ON THE MARINE ALGAE OF PUERTO RICO. IV.  
THE TAXONOMIC PLACEMENT OF *GRALLATORIA*  
(CERAMIACEAE, RHODOPHYTA)

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ABSTRACT. — Observations are made on Puerto Rican collections of the red algal genus *Grallatoria* Howe, based on the type *G. reptans*. Evidence is presented that this genus is best assigned to the tribe Wrangelieae (Ceramiaceae, Ceramiales) on the basis of the origin of indeterminate branches from the basal cell of a whorl-branch, uninucleate vegetative cells, tetrahedrally divided tetrasporangia, involucrate cystocarps, and the production of spermatangial heads. It is argued that *Grallatoria* and *Callithamniella* Feldmann-Mazoyer are not congeneric, confirming the opinion of SCHNEIDER (1984).

RÉSUMÉ. — Le genre *Grallatoria* Howe (Rhodophyta), fondé sur le type *G. reptans*, a été étudié à partir de collections réalisées à Puerto Rico. Plusieurs caractères conduisent à rattacher ce genre à la tribu des Wrangelieae (Ceramiaceae, Ceramiales) : développement des rameaux à croissance indéfinie à partir de la cellule basale d'un des rameaux du verticille, cellules végétatives uninucléées, tétrasporocystes tétraédriques, cystocarpes entourés de filaments involucreux, spermatocystes disposés « en manchon ». L'opinion de SCHNEIDER (1984), est confirmée : *Grallatoria* et *Callithamniella* Feldmann-Mazoyer ne sont pas congénériques.

KEY-WORDS : *Callithamniella*, Ceramiaceae, *Grallatoria reptans*, marine algae, Puerto Rico, Rhodophyta, *Wrangella dumontii*.

#### INTRODUCTION

*Grallatoria reptans* Howe (1920), a monotypic genus of the Ceramiaceae (Rhodophyta) endemic to the Caribbean, has been seldom reported since its description from the Bahamas. It was still known only from the original account when TAYLOR's (1960) floristic treatment appeared. ABBOTT (1976) has since reported its presence at St. Croix in the U. S. Virgin Islands. The present account is the first record of this species from Puerto Rico.

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In ABBOTT's (1976) study of *Grallatoria*, she described spermatangia and cystocarps for the first time and concluded that the genus can be tentatively assigned to the tribe Sphondylothamnieae on the basis of vegetative and reproductive features. She also made a case for regarding *Callithamniella* of FELDMANN-MAZOYER (1938, 1939) as con-generic with the earlier described *Grallatoria* and transferred two species of *Callithamniella* into *Grallatoria*.

On the basis of his North Carolina collections of *Callithamniella tingitana* (Schousboe ex Bornet) Feldmann-Mazoyer, the type of that genus, SCHNEIDER (1984) maintained *Callithamniella* as a distinct genus. His contention for keeping these two genera separate was based on the fact that indeterminate axes never arise on determinate axes in *Grallatoria reptans*. Our collections of *Grallatoria reptans* from Puerto Rico have permitted us to re-investigate these problems, regarding both the relationship between *Grallatoria* and *Callithamniella* and also the placement of *Grallatoria* within the family Ceramiaceae.

### MATERIALS AND METHODS

This study is based on the following collections of *Grallatoria reptans* made in Puerto Rico, all by D.L. Ballantine : edge of insular shelf off La Parguera : DLB 2080, 19.v.1977, 18 m, on coral rubble; DLB 2, 18.xii.1978, on *Verongia*; DLB 167, tetrasporic, 30.iii.1979, 20 m, on *Verongia*; DLB 536, 12.x.1979, on *Verongia*. Seaward of Media Luna Reef : DLB 2031, tetrasporic, 28.ii.1978, 18 m, epiphytic. Desecheo Island : DLB 1395, 18.x.1980, 18 m, on *Verongia*. Voucher specimens have been deposited in the herbaria of the Dept. of Marine Sciences, Univ. of Puerto Rico (MSM) and of the Univ. of Michigan (MICH).

Observations of *Wrangelia dumontii* (Daws.) Abbott (*Anthithamnion dumontii* Daws.) were made on specimens on loan from the U.S. National Museum (US), all Dawson collections : Panama, Isla Jicarón : EYD 21128 (holotype), 25.iii.1959; Isla Brincanco Bay, Islas Contreras : EYC 21406, 26.iii.1959. Costa Rica, Isla del Caño : EYD 21066, 28.iii.1959; EYD 21085a, 28.iii.1959.

Collections were preserved in 4% formalin-seawater. Slides were prepared by staining in a mixture of 1% aniline blue/1N HCl/Karo syrup/water (4:1:20:75). For nuclear staining Delafield's haematoxylin was used. A standard Zeiss research microscope equipped with a camera back and a camera lucida was used.

### OBSERVATIONS

Puerto Rican plants of *Grallatoria reptans* are found growing as epiphytes as well as on hard substrata at moderate depths (to 20 m). The organization of these thalli is in full agreement with the description given by HOWE (1920), in which a pair of opposite lateral ramuli is produced at the distal end of each segment of the repent (main) axis. These opposite ramuli are whorl-branches. Each of these oppositely placed ramuli branch at their basal cell, producing

an erect simple filament and a descending multicellular hapteron (Fig. 3, 9 and 10). The multicellular rhizoids produced by the pair of lateral whorl-branches are usually elaborately digitate at their distal ends, and they permit the creeping axis to be lifted off the substrate (Fig. 1 and 11), as a «stilt-walker», as observed by HOWE (1920) and ABBOTT (1976).

Typically, on every other segment of the repent axis there is a third determinate whorl-branch (Fig. 1 and 2), the «dorsal erect ramuli» of HOWE (1920). The dorsal whorl-branch is much branched, more robust, and is of greater height (1.4 mm) than the erect portions from the oppositely placed lateral whorl-branches (Fig. 1). It is also formed prior to the lateral whorl-branches. It is on the basal cell of this dorsal erect ramulus that the indeterminate branches originate, as a bulge from the distal end of that basal cell. This basal cell is different in appearance from the succeeding cells (Fig. 9 and 10), in that the basal cell is at the most twice as long as broad. The succeeding cells (at maturity) are up to six times as long as broad, as HOWE (1920) also observed. Occasionally two adjacent segments of a repent axis produce dorsal ramuli.

Apical cells of indeterminate axes are relatively small and are densely surrounded by the young whorl-branches (Fig. 1 and 11). Vegetative cells are uninucleate. Filaments of different ages were stained with hematoxylin, and there was invariably a single nucleus per cell (Fig. 5, 7 and 8).

The only reproductive stages observed in the Puerto Rican collections were tetrasporangiate thalli. Tetrasporangia are pedicellate and are produced on the dorsal whorl-branches (Fig. 4 and 6). They are tetrahedrally divided, ovoid, 24-34  $\mu\text{m}$  in length and 18-25  $\mu\text{m}$  in width at maturity. There are no involucrel filaments associated with the tetrasporangia.

Since ABBOTT (1979) pointed out many similarities between *Grallatoria reptans* and *Wrangelia dumontii* (Daws.) Abbott, both of them being dorsiventrally organized «stilt-walkers», we have examined material used by DAWSON (1960) in his description of *Antithamnion dumontii*, the basionym of *W. dumontii*. Like *G. reptans*, *W. dumontii* is primarily a creeping alga (Fig. 12). We have observed typically four whorl-branches per axial cell of the repent (indeterminate) axes, the two whorl-branches on the ventral side being different in appearance from the two dorsal whorl-branches (Fig. 13 and 17). Multicellular rhizoids develop from the basal cell of each ventral whorl branch, and often the proximal cells of these rhizoids are inflated (Fig. 12). Indeterminate branches originate from the basal cell of one of the pair of dorsal whorl-branches (Fig. 14 and 16). The indeterminate branches often arise on consecutive segments of a creeping axis (Fig. 15); they repeat the pattern of organization of the parent axis.

In the material of *Wrangelia dumontii* examined, both tetrasporangia and spermatangial heads were observed to be surrounded by involucrel filaments, as noted by ABBOTT (1979) and SCHNETTER & BULA MEYER (1982). These reproductive structures occurred on the dorsally placed whorl-branches.

## DISCUSSION

It is significant that the arrangement and pattern of formation of the determinate and indeterminate branches in the Puerto Rican material of *Grallatoria reptans* is remarkably constant. HOWE (1920) did not make a distinction between whorl-branches and indeterminate branches, nor did he determine the origin of indeterminate branches. But he did observe that lateral «ramuli» (= whorl-branches) were produced from essentially every segment of the «primary filament» (= indeterminate branch) and that a dorsal erect ramulus, 1-4 mm high, was produced «usually from every second segment of the primary filament». We entirely concur with Howe's observations with the additional point: the basal cell of the dorsal whorl-branch («ramulus») is the point of origin of an indeterminate branch, or primary filament.

Thus, we cannot agree with ABBOTT's (1976) characterization of this alga as having a «not necessarily fixed» order of occurrence and arrangement of haptera and determinate and indeterminate branches. Abbott noted that indeterminate branches sometimes arise «adventitiously» from the lowest cell of an indeterminate branch (her fig. 2). It is our opinion that the dorsal branch is undoubtedly a determinate branch, namely, the third whorl-branch, which is better developed than the two laterally placed whorl-branches. We also find that indeterminate branches arise from the basal cell of the dorsal whorl-branch; thus, it does not arise adventitiously. Abbott's fig. 1 and 2 depict the production of indeterminate branches from the basal cell of the dorsal whorl-branch in an early (fig. 2) and a later stage (fig. 1).

*Grallatoria* demonstrates several characteristics that indicate a relationship with *Wrangelia*, the only member of the tribe Wrangelieae (GUIRY, 1978). The following shared traits are evidence of the close relationship between these two genera:

- 1) uninucleate vegetative cells. The uninucleate condition persists in vegetative cells even as they enlarge and mature (Fig. 8). It is known that only certain tribes of Ceramiaceae are characterized by the multinucleate condition in the fundamental sense that the apical cells are multinucleate (L'HARDY-HALOS, 1971). GORDON (1972) and WYNNE (1980) demonstrated that the nuclear condition of vegetative cells is a useful taxonomic feature at the tribe level. Vegetative cells are uninucleate in the Wrangelieae but are multinucleate in the Sphondylothamnieae (GORDON, 1972).

- 2) cystocarps surrounded by involucrel filaments involving the whole terminal portion of a fertile branch. Compare ABBOTT's (1976) fig. 5 (for *Grallatoria reptans*) with GORDON's (1972) fig. 3A (for *Wrangelia princeps*). The intermingling of fertile and sterile filaments in the development of the cystocarp, which is stated to be a distinctive feature of the Wrangelieae (GORDON, 1972, p. 14 & 154), appears to also be the condition in *Grallatoria* on the basis of ABBOTT's (1976) characterization. Our collections did not include cystocarpic thalli.

- 3) relatively small apical cells of indeterminate axes, surrounded by young whorl-branches. This is in agreement with *Wrangelia* but in contrast to the condi-

tion in the Sphondylothamnieae, which have large apical cells not protected by long whorl-branches (GORDON, 1972).

4) the development of indeterminate branches from the basal cells of whorl-branches. We interpret the dorsal ramulus (from every other segment) and the pair of lateral ramuli (from every segment) to be whorl-branches in *G. reptans*. The dorsal ramulus is much better developed (to 4mm) than the lateral ramuli, but both types are determinate. The indeterminate branches arise on the basal cell of the dorsal ramulus, and that is the only point of origin for indeterminate branches. GORDON (1972) has listed this feature as one of the primary characteristics of the Wrangelieae and as a difference from the Sphondylothamnieae. Although ABBOTT (1979) did not recognize this fact in *W. dumontii*, we have observed that indeterminate branches in that species also originate from the basal cell of an erect whorl-branch, in agreement with other species in the genus.

5) spermatangial heads are produced in both *Wrangelia* (GORDON, 1972; ITONO, 1977; ABBOTT, 1979) and *Grallatoria* (ABBOTT, 1976). ITONO (1977) regarded these compact spermatangial heads in the Wrangelieae to resemble those in advanced tribes, thus an apomorphic character (ELDREDGE & CRACRAFT, 1980).

6) tetrahedrally divided tetrasporangia produced in lower cells of the whorl-branches (on only the dorsal whorl-branches in *Grallatoria*).

7) a distinctive purple color. Species of *Grallatoria* are invariably referred to as being deep purplish-red, purple, or purplish-blue in color (TSENG, 1942; TAYLOR, 1960; GORDON, 1972). It is noteworthy that HOWE (1920) described the color of *G. reptans* as «vinaceous-purple to dark vinaceous-brown (near the color of *Wrangelia Argus*)».

8) the dorsal ramulus is cut off first, followed by the lateral ramuli, resulting in a zig-zag pattern. CHADEFAUD (1954) demonstrated a scorpioid, or zig-zag, manner of formation of the whorl-branches in *Wrangelia penicillata*, and such a distinctive pattern appears to be characteristic of the Wrangelieae (M. Hommersand, *in litt.*).

It would appear that dorsiventral organization, non involucrate spermatangial heads, and the lesser number of whorl-branches in *Grallatoria* would distinguish it from *Wrangelia*. Closer examination, however, reconciles these differences. Although GORDON (1972, p. 13) characterized the tribe Wrangelieae as having «erect axes only», the thalli of some species in *Wrangelia* have been described as creeping, prostrate, or dorsiventral. GORDON (1972) indicated two lines within the genus in which dorsiventral and flattened thalli are attained (*viz.*, *W. nobilis* and *W. australis*). ABBOTT (1979) described *St. Croix* specimens of *W. argus* as being «at least half decumbent». The same species has been said to be «partly prostrate» in Great Barrier Reef populations (CRIBB, 1983) and to be «mostly prostrate plant» in South African populations (NORRIS and AKEN, 1985). The transfer of *Antithamnion dumontii* DAWSON (1960) into *Wrangelia* by ABBOTT (1979), a species with a creeping, dorsiventral habit, is an additional example. Thus, it appears that *Grallatoria reptans*, with its creeping, dorsiventral habit, is no longer remote from the Wrangelieae.

According to ABBOTT (1979) a difference between *Grallatoria reptans* and *Wrangelia dumontii* is that tetrasporangia are allegedly cruciately divided in the former and tetrahedrally divided in the latter. This difference can be discounted, however, since the sporangia are indeed tetrahedrally divided in *G. reptans*, as stated by HOWE (1920) and ABBOTT (1976) in her earlier report and as observed in this study (Fig. 4 and 6).

The lack of involucrel filaments around the spermatangial heads and tetrasporangia in *Grallatoria* differs from the involucrel condition in the majority of species of *Wrangelia*. However, this generalization is not true for all species of that genus. Special involucrel filaments around the tetrasporangia are not present in *W. princeps* (GORDON, 1972). This fact again diminishes the separation between *Grallatoria* and the *Wrangeliaceae*.

Although five is the usual number of whorl-branches per axial cell in *Wrangelia* (GORDON, 1972), several species are known to have only four whorl-branches per axial cell. Although ABBOTT (1979) asserted in *W. dumontii* that there are only three whorl-branches per axial cell, «4 if indeterminate branch is added» (ABBOTT, 1979), our observations revealed that four whorl-branches per axial cell is the usual number in that species. SCHNETTER and BULA MEYER (1982) also observed four verticillate branches from each segment of the creeping axis. Typical for the genus, the indeterminate branch arises on the basal cell of one of the whorl-branches in *W. dumontii* (namely, one of the erect whorl-branches). Likewise, in regard to CRIBB's (1983) characterization of *W. argus* as having four branch systems per node of the main axis, «3 of the 4 systems determinate, 1 indeterminate», we interpret this to mean that there are 4 determinate branches (whorl-branches) per axial cell of the indeterminate axis, with the new indeterminate branch system arising from the basal cell of one of the whorl-branches, as is true for the genus (GORDON, 1972; ITONO, 1977). This distinctive manner of initiation of indeterminate branch formation, which is known in all species of *Wrangelia* and in *Grallatoria reptans*, is a strong argument for relating these two genera.

It is our opinion that *G. reptans* should be maintained in its own genus separate from *Wrangelia* because of only 2 (or 3) whorl-branches per axial cell, the precise pattern of two whorl-branches per axial cell with a third (dorsal) whorl-branch on alternate axial cells, its strongly dorsiventral organization, and its lack of involucrel filaments around the spermatangial heads and tetrasporangia.

In light of our observations that the indeterminate branches arise from the basal cell of a whorl-branch, it is necessary to re-examine SCHNEIDER's (1984) discussion of the relationship between *Grallatoria* and *Callithanniella*. SCHNEIDER (1984) accepted ABBOTT's (1976) statement that indeterminate axes never arise on determinate axes and employed that distinction to maintain these as two separate genera, contrary to Abbott's merger of these two taxa. Thus, the present observations preclude that characteristic as a means to discriminate these two taxa. There are, however, other differences which are present to maintain these two genera as distinct. Foremost is the fact that tetrasporangia

are cruciately divided in *Callithamniella* (FELDMANN-MAZOYER, 1939) but tetrahedrally divided in *Grallatoria* (HOWE, 1920; ABBOTT, 1976; present observations). Indeterminate axes in *Callithamniella tingitana* bear laterals singly or in pairs in an irregular sequence (FELDMANN-MAZOYER, 1938; SCHNEIDER, 1984), whereas indeterminate axes in *Grallatoria reptans* bear whorl-branches in pairs or in whorls of three in a very precise alternating sequence (HOWE, 1920; present observations). In both taxa rhizoids originate from the basal cell of a lateral/whorl-branch; in *C. tingitana* these rhizoids are most often depicted as being unicellular (FELDMANN-MAZOYER, 1938; JOLY, 1965; SCHNEIDER, 1984) but as multicellular in *G. reptans* (ABBOTT, 1976; present observations). These differences argue for maintaining *Callithamniella* and *Grallatoria* as separate genera.

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## LEGENDS FOR PLATES

Fig. 1-4 : *Grallatoria reptans*. Fig. 1. Habit of creeping axis raised above substrate by rhizoids. Fig. 2 and 3. Formation of dorsal ramulus from alternate segments and origin of indeterminate branch from basal cell of dorsal whorl-branch. Fig. 4. Production of tetrasporangia on dorsal whorl-branch. Scale bars : 50  $\mu\text{m}$  in Fig. 1-3; 20  $\mu\text{m}$  in Fig. 4.

Fig. 5-10. *Grallatoria reptans*. Fig. 5, 7, and 8. Cells of different ages, with nuclei stained. Fig. 6. Portion of a dorsal whorl-branch bearing tetrasporangia. Fig. 9 and 10. Segment with one whorl-branch (of the pair) and a dorsal whorl-branch with the dorsal whorl-branch bearing an indeterminate branch from its basal cell (*bc*). Note the difference in size between the basal cell and the suprabasal cell (*sb*) of the dorsal whorl-branch.

Fig. 11-17. Fig. 11. *Grallatoria reptans*. Fig. 12-17. *Wrangelia dimontii*. Fig. 11. Habit. Fig. 12. Habit. Fig. 13-16. Formation of rhizoid from basal cell of ventral whorl-branch and formation of indeterminate branch from basal cell of dorsal whorl-branches. Fig. 17. Formation of indeterminate branches from successive dorsal whorl-branches. Scale bars : 50  $\mu\text{m}$  in Fig. 11-13 and 15; 30  $\mu\text{m}$  in Fig. 14 and 17; 20  $\mu\text{m}$  in Fig. 16.







